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NICHE OVERLAP DETERMINATION THROUGH HABITAT SUITABILITY MODELS: A MANAGEMENT TOOL FOR NATIVE BIRDS OF THE ARGENTINEAN PAMPAS

DETERMINACIÓN DE LA SUPERPOSICIÓN DE NICHO MEDIANTE MODELOS DE ADECUACIÓN DE HÁBITAT: UNA HERRAMIENTA DE MANEJO PARA AVES NATIVAS DE LA PAMPA ARGENTINA

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SUMMARY.—In Argentina, predominantly in the Pampas ecoregion, the natural rangelands have increasingly been replaced by crops. Avifaunal studies have shown that the population density of several species decreased as the proportion of cropland in the landscape increased. The Greater Rhea *Rhea americana* and two migratory sheldgeese: the Upland Goose *Chloephaga picta* and Ashy-headed Goose *Chloephaga poliocephala*, are medium-large native species that have been common and sympatric inhabitants of the Pampas ecoregion. We aimed to analyse and compare the current ecological niches occupied by the three species during the non-breeding season in the southern Pampas of Argentina, the region where their original distributions overlapped, using Ecological Niche Factor Analysis. The three species showed high global marginality values, indicating that they occupied only a specific subset of environmental conditions of those available across the region. Suitable areas for Greater Rhea were located in the west and south of the study area, overlapping grazing lands and native habitats. The three species responded to landscape composition and configuration, as indicated by the low proportion of areas with suitable conditions for these medium-large birds. Suitable areas for Ashy-headed and Upland Geese were especially concentrated in the eastern part of the area and suitable areas for Upland Goose were more widespread than those suitable for the Ashy-headed Goose. We provide compelling evidence of low overlap between the ecological niches of the three species in the southern Pampas, which highlights the need for specific management strategies to ensure the conservation of these emblematic species. —Pedrana, J., Bernad, L., Maceira, N.O. & Isacch, J.P. (2018). Niche overlap determination through habitat suitability models: a management tool for native birds of the Argentinean Pampas. *Ardeola*, 65: 25-40.

Key words: agroecosystem, Ashy-headed Goose, ecological niche, grassland, Greater Rhea, Upland Goose.

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RESUMEN.—En Argentina, predominantemente en la ecorregión de las Pampas, los pastizales naturales han sido cada vez más reemplazados por cultivos. Estudios de la avifauna han demostrado que la densidad poblacional de varias especies disminuyó a medida que aumentaba la proporción de tierras cultivadas en el paisaje. El ñandú común *Rhea americana,* el cauquén común *Chloephaga picta* y el cauquén cabecigrís *Chloephaga poliocephala* son especies nativas de mediano tamaño que han sido habitantes abundantes y simpátricos de la ecorregión pampeana. Nuestro objetivo fue analizar y comparar el actual nicho ecológico ocupado por estas tres especies durante la época no reproductiva en el sur de la región pampeana, utilizando un Análisis de Factor de Nicho Ecológico (ENFA). Todas las especies mostraron altos valores de marginalidad global, indicando que sólo ocupan un conjunto específico de condiciones ambientales disponibles en el área estudiada. Las áreas más adecuadas para el ñandú común se localizaron en el oeste y sur del área de estudio, solapándose con campos de pastoreo y pastizales. Las tres especies respondieron a la composición y configuración del paisaje, como lo indica la baja proporción de paisaje con condiciones adecuadas para estas aves. Las áreas adecuadas para los cauquenes se concentraron especialmente en la zona oriental del área de estudio, siendo que las áreas para el cauquén común fueron más grandes en comparación con el cauquén cabecigrís. En este estudio, se proporciona una fuerte evidencia de que actualmente hay un bajo solapamiento entre los nichos ecológicos de las tres especies, lo cual pone de manifiesto la necesidad de generar estrategias de manejo específicas para contribuir a la conservación de estas especies emblemáticas. —Pedrana, J., Bernad, L., Maceira, N.O. e Isacch, J.P. (2018). Determinación de la superposición de nicho mediante modelos de adecuación de hábitat: una herramienta de manejo para aves nativas de la Pampa argentina. *Ardeola*, 65: 25-40.

Palabras clave: agroecosistema, cauquén común, cauquén cabecigrís, nicho ecológico, ñandú común, pastizal.

INTRODUCTION

Identifying important areas for biodiversity conservation is essential for directing the management of natural resources. Fundamentally, we must know where species live, which are more susceptible to extinction, where human actions threaten them and what levels of protection they are receiving (Jenkins *et al*., 2013). In particular, knowledge of the distribution of declining bird species and their habitat requirements is essential in conservation biology.

Habitat loss and fragmentation due to land use have long been recognised as major threats to the preservation of biodiversity and to the viability of endangered or vulnerable species (Collingham & Huntley, 2000; Azpiroz *et al*., 2012). Loss and degradation of grasslands have negatively affected bird populations worldwide (Collar *et al*., 1992). In North America, 75% of grassland birds have suffered population declines over the last 30 years (Askins *et al*., 2007; Brennan *et al*., 2012). In Europe, 70% of grassland and steppe species have also undergone drastic population reductions due to changes in agricultural practices (Donald *et al*., 2006; Kleijn *et al*., 2009). In South America, 22 grassland species are considered globally threatened or near-threatened (IUCN, 2017) and many others are considered in peril at national or regional levels (Azpiroz *et al*., 2012).

Studies of the avifauna have shown that the population density and distributional range of several species decreased as the proportion of croplands in the landscape increased (Schrag *et al*., 2009; Cerezo *et al*., 2011). Populations of most of these grassland birds have declined markedly or are now fragmented (Codesido *et al*., 2011; Azpiroz *et al*., 2012). For instance, based on historic and current records for Buenos Aires province, Narosky & Yzurieta (2010) identified several species that are thought to have either declined in numbers or disappeared from certain areas, these including the Greater Rhea (Bucher & Nores, 1988; Giordano *et al*., 2008). Populations of long-distance migratory birds, such as two sheldgeese species, the Upland Goose and Ashy-headed Goose, also show evidence of recent declines within their wintering areas in the Pampas ecoregion (IUCN, 2017). These medium-large birds were formerly common and sympatric inhabitants of the Pampas ecoregion (Figure 1a; Hudson, 1920; Bucher & Nores, 1988; Narosky & Yzurieta, 2010). In comparison to other grassland species, the Greater Rhea and these two species of migratory sheldgeese exhibit a broader distributional range and show a selective use of habitats (Bellis *et al*., 2004a; Pedrana *et al*., 2014, 2015a). Regional scale studies of habitat use show that all species avoid areas near villages and cities, and the Greater Rhea mostly inhabits agroecosystems that include grasslands and pastures (Bellis *et al*., 2008; Giordano *et al*., 2010; Pedrana *et al*., 2015a), while the Ashy-headed Goose and Upland Goose use areas dominated by crops (Martin *et al*., 1986; Pedrana *et al*., 2014) more often than Greater Rhea.

In Argentina, predominantly in the temperate grasslands ecosystems of the Pampas ecoregion, the most human-modified habitat in the country, the natural rangelands have increasingly been replaced by croplands and sown pastures for livestock, with a notable expansion of soybean cultivation (Baldi & Paruelo, 2008). The area cultivated with soybean has grown from 5 Mha in 1994 to 20 Mha in 2014, covering 65% of the cultivated lands in this country (FAOSTAT, 2014). The growing environmental transformation of the Pampas ecoregion will probably result in further changes in bird population dynamics, including declines or even regional extinction of populations (Isacch *et al*., 2005; Codesido *et al*., 2011; Azpiroz & Blake, 2016). This situation has become especially critical for the species mentioned, for which poaching and violation of hunting regulations are additional problems (Blanco & de La Balze, 2006; Giordano *et al*., 2010). The International Union for Conservation of Nature (IUCN) has classified the Greater Rhea as Near-threatened and Upland Goose and Ashy-headed Goose as Least Concern globally (IUCN, 2017). However, in Argentina, the Greater Rhea and Ashy-headed Goose are classified as Endangered, and the Upland Goose as Vulnerable (López-Lanús *et al*., 2008), indicating their urgent need for conservation and the implementation of management actions in rural areas.

To conserve biodiversity it is imperative to understand how different species respond to land use change. Some authors have described the ecological niche occupied by a certain species as the variation in habitat suitability values throughout the environmental gradient (Cassinello *et al*., 2006; Acevedo *et al*., 2007). Ecological Niche Factor Analysis (ENFA) is an analytical tool that describes the multidimensional space where a species occurs and compares it with the conditions existing in the study area (Hirzel *et al*., 2002). The multidimensional space is described by a number of uncorrelated factors that have a direct interpretation in the species' ecological niche. The resulting distribution models are used to build habitat-suitability models that are then translated over the whole study area, generating habitat-suitability maps (Hirzel *et al*., 2002). ENFA's main advantages in comparison to other statistical frameworks is that the results are useful to compare different species that overlap spatially within a certain region (Hirzel & Le Lay, 2008).

In this context, one of our aims was to use ENFA to analyse and compare the current ecological niches occupied by the Greater Rhea (GR), Ashy-headed Goose (AG) and Upland Goose (UG) during the non-breeding season in the southern Pampas of Argentina, the region where their original distributions overlapped (Figure 1a). At the same time, we wanted to test the hypothesis that differential habitat use by birds and their life histories (e.g. migratory vs non-flying resident species) could reflect contrasting species' responses to habitat conditions and human pressures in the Pampas ecoregion. This hypothesis predicts that habitat transformation could have impacted less strongly on both sheldgeese than on Greater Rheas. This could be due to the former's ability to escape human persecution by flying away and their preference for cultivated fields and migratory behaviour, which makes them less dependent on the Pampas region for survival.

Methods

Study Area

The study area represented more than a third of the main historical area of overlap between the studied species (Figure 1a). It coincides with the southern range of the Greater Rheas' distribution and the wintering area of migratory Ashy-headed and Upland Geese. This territory is the southeast region of Buenos Aires province, Argentina (81,000 km^2) corresponding to the southern Pampas ecoregion (between 36.46° to 41.04°S and 63.39° to 58.62°W) (Soriano *et al*., 1992). It has a sub-humid mesothermal climate (mean annual temperature 10-20 °C and mean annual rainfall 400-1,000 mm), and includes the mountains of the Ventania System and a coastal plain with a moderate slope to the Atlantic Ocean. Pristine vegetation was dominated by several species of *Stipa* and *Piptochaetium* spp. (Soriano *et al*., 1992). Currently, most of the original grasslands have been replaced by pastures and croplands (Baldi & Paruelo, 2008).

Species Occurrence Data

We used occurrence data collected through road-based surveys performed from June to July 2011 and June to July 2012 (i.e. the non-breeding season). Surveys were conducted from a vehicle driven at a maximum speed of 50 km/hr along 110 survey tracks selected randomly, amounting to 4,600 km of secondary road transects during the first year. The same tracks were surveyed in the second year.

When one of the species was encountered, we stopped the vehicle, registered our position using a GPS and measured the distance to the sighting with a laser rangefinder and the angle of the bird relative to our bearing. From these measurements, we determined the actual positions of the sighting (Travaini *et al*., 2007).

All survey tracks were overlaid on a grid of 1-km grid cells. We surveyed a total of 7100 cells (9% of the whole study area). Sightings of each species were also overlaid, and grid cells with more than one sighting were considered a presence. The presence raster map was divided into two data sets. Each presence registered in 2011 (AG = 69, UG = 143 and GR = 76) was used to calibrate the models and presences registered in 2012 (AG = 58, UG = 113, GR = 70) served to validate it (see Ecological Niche Factor Analysis).

Environmental Variables

We used 1-km grid cells to characterise the study region using 17 variables (Table 1). A land-cover map was constructed for the study area based on four parameters of the normalised difference vegetation index (NDVI) curves derived from satellite MODIS images (Moderate Resolution Imaging Spectroradiometer) (using 24 scenes from June 2011 to July 2012). The parameters were 1) the Integrative Normalized Difference Vegetation index corresponding to the sum of positive NDVI values (NDVII), 2) Annual maximum values of the NDVI (Max NDVI), 3) Annual minimum values of the NDVI (Min NDVI) and 4) variability in productivity: (Max

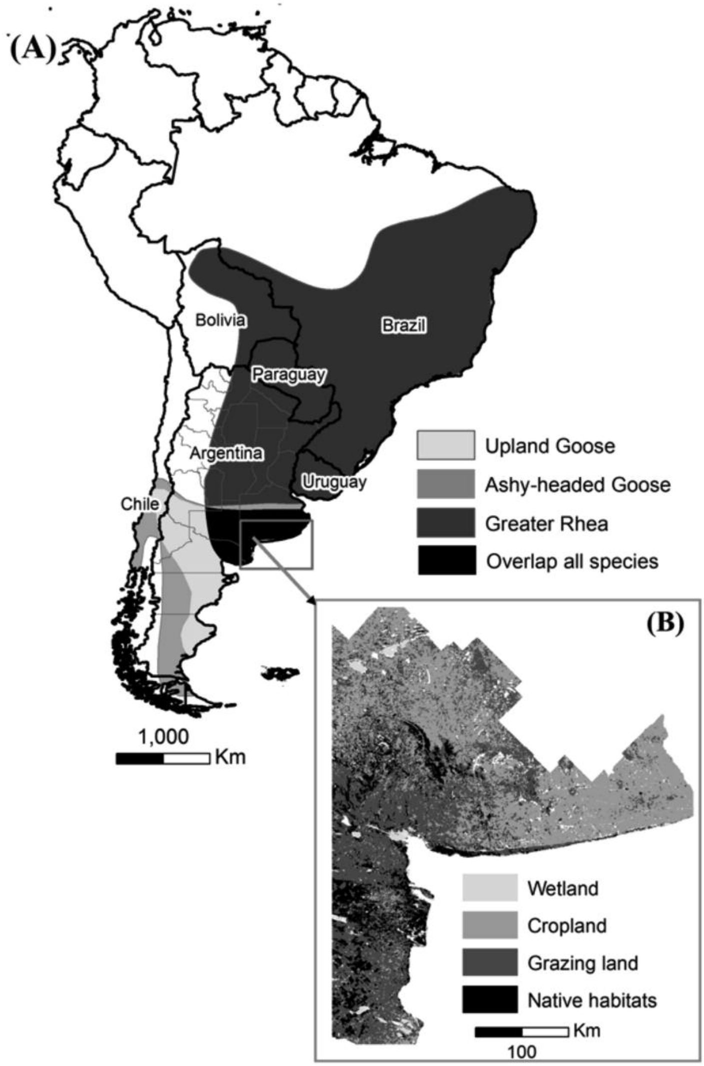

FIG. 1.—a) Historical regional distribution of Greater Rhea, and non-breeding grounds for Upland Goose and Ashy-headed Goose, showing sympatric areas of the three species (dark areas) (Redrawn from IUCN, 2017). The inset (b) describes the location of the study area that includes the main area of overlap on the southern Pampas, Argentina. Different colours indicate the four main habitat categories (cropland, grazing land, native habitat and wetland) (see "Environmental variables"). See supplementary material appendix 1, Figure A1 for a colour version.
[Distribución regional histórica del nandú y de las áreas de invernada del cauquén común y el cauquén cabecigrís, donde se muestran las áreas simpátricas de las tres especies (áreas oscuras), (Rediseñado de la UICN, 2017). La inserción (b) describe la ubicación de la zona de estudio que incluye la principal zona de superposición en el sur de la región Pampeana, Argentina. Diferentes colores indican las cuatro principales categorías de hábitat (cultivos, campos de pastoreo, hábitat nativo y humedales), (véase la subsección "Variables del paisaje"). Veáse el material suplementario, apéndice 1, Figura A1 para una versión en color.]

NDVI – Min NDVI) / NDVII. These parameters have been reported as a plausible way of describing vegetation parameters relevant to wildlife (Pettorelli *et al*., 2005) and of capturing important features of ecosystem functioning for temperate ecosystems (Paruelo *et al*., 2001; Pedrana *et al*., 2014). We used a procedure that combines the generation of different clusters (through ISODATA, IDRISI Selva, Eastman, 2012) and *a posteriori* assigned these clusters to four habitat categories: cropland, grazing land (principally, sown pastures), native habitat (natural grasslands and scrublands, degraded in general) and wetland (Table 1, Figure 1b). An error matrix was created to test the accu-

TABLE 1

Description of the environmental variables used in ENFA generated for Greater Rhea, Upland Goose and Ashy-headed Goose in the southern Pampas, Argentina.
[Descripción de las variables ambientales utilizadas en el ENFA para el ñandú común, el cauquén común y el cauquén cabecigrís en el sur de la región Pampeana, Argentina.]

Variable	Description
Altitude	M.a.s.l. obtained from the SRTM.
Slope	Terrain slope acquired from the SRTM.
Dist.stream	Distance to the closest river, acquired from Instituto Geográfico Nacional (IGM), Argentina.
Dist.lake	Distance to the closest waterbody, acquired from IGM, Argentina.
Dist.urban	Distance to the nearest urban centre, acquired from IGM, Argentina.
Crop.area Grazing.area Native.area Wetland.area	Sum of cells of each habitat type: cropland, grazing land (principally, sown pastures), native habitat (natural grasslands and scrublands, in general degraded) and wetland patches in a circle of 1.8-km radius around a focal cell.
Crop.edge Grazing.edge Native.edge Wetland.edge	Sum of the lengths of all edge segments involving habitat type patches in a circle of 1.8-km radius around a focal cell.
Crop.con Grazing.con Native.con Wetland.con	Percentage of cell adjacencies involving the same habitat type as the one in the focal cell, in a circle of 1.8-km radius, as a measure of connectivity.

racy between cluster assignation and current land-cover types based on 850 control points that were taken during the road-based surveys. We obtained an overall accuracy of 78% and the users' accuracy (error of commission) was 80%, 74%, 70%, and 80% for wetland, grazing land, native habitat and cropland, respectively. The overall Kappa Statistic was 0.7.

Since the perception of the landscape by birds is commonly associated with their home-range size (Bellis *et al*., 2004b; Pedrana *et al*., 2015b), we included one neighbourhood scale related to the estimated home-range size of all species: circles of 10 km^2. We then extracted three indexes from the land-use map with Fragstats (McGarigal *et al*., 2012): edge density and total class area for each habitat type and percentage of cell adjacencies involving the same habitat type as that in the focal cell, as a measure of connectivity between patches of the same habitat type (Table 1). Distances from each 1-km cell to the nearest urban settlement, the nearest waterbody (lakes and ponds) and the nearest rivers and streams (taken from Instituto Geográfico Nacional, Argentina, http://www.ign.gob.ar) were calculated in a GIS. Topographic data (altitude and slope) were acquired from the Shuttle Radar Topography Mission (SRTM; http://www2.jpl.nasa.gov) (Table 1).

Ecological Niche Factor Analysis

We analysed the ecological niche of each species across the study area using ENFA, which calculates a set of new uncorrelated factors from the available variables. The first factor (the marginality factor) accounts for all the marginality, whereas the others refer to specialisation (specialisation factors). The marginality factor is defined as the distance between the species optimum and the mean habitat within the reference area. Hence, a high marginality value (≥ 1) indicates that the species' requirements differ considerably from the average habitat conditions in the area and a value close to zero shows that the species is found everywhere (Hirzel & Le Lay, 2008). The specialisation factors are defined as the relationship between the residual variance of the background data and the variance of the species' occurrences. In specialisation factors, the higher the absolute value (≥ 1), the more restricted the range of the focal species on the corresponding variable in relation to the available range in the study area (low tolerance; Hirzel *et al*., 2002; Falcucci *et al*. 2009). We implemented ENFA using Biomapper 4.0 software (Hirzel *et al*., 2002).

Habitat Suitability Maps

Factors generated by ENFA were used to construct habitat suitability maps (HSM) for each species. We used 'MacArthur's broken-stick distribution' for selecting the number of factors and the 'median + extreme' algorithm (i.e. where the optimum of the species is expected to be around the highest or the lowest values of the variable) to consider in HSM (Braunisch *et al*., 2008; De Angelo *et al*., 2011). Model evaluation was done by applying a jack-knife cross-validation procedure using 10-fold, which is used to build a curve to observe the relationship between the mean predicted/expected ratio (P/E) of independent validation data (Hirzel *et al*., 2006). We examined these curves in order to reclassify HSMs in three categories of habitat quality: unsuitable (P/E = 0; no records of the species under this condition), marginal (0 < P/E ≤ 1; the model predicts fewer presences than expected by chance) and suitable (P/E > 1; the model predicts more presences than expected by chance) (De Angelo *et al*., 2011). Since one of the goals was to compare ecological niches between species, we decided to use only three categories with clear defined thresholds. Model evaluation was also done by calculating the Boyce index that ranges from 0 (when model discrimination is not better than random) to 1 (indicating a consistent model with high predictive ability) (Boyce *et al*., 2002).

Niche Overlap

In order to compare interspecific differences in the variables selected for each species, discriminant analyses were performed between the ecological niches of species-pairs (Ayala *et al*., 2009). While the ENFA compared the distribution of variables where a species was present with the conditions in the whole area, discriminant analysis compared the distribution of variables that defined the ecological niche of two species.

We overlapped the categorised HSM of the three species using a cross-tabulated analysis in a GIS environment (IDRISI Selva), taking into account only two categories of habitat quality (marginal and suitable). As a result of the cross-tabulated analysis, we identified areas of spatial coincidence (areas suitable or marginal for all species) and non-coincidence (suitable for some species and marginal for others).

Results

Ecological Niche Factor Analysis

One of the most significant results was the high global marginality value found for all the species (marginality = 0.95 for UG, marginality = 1.05 for GR and marginality = 1.45 for AG), indicating that these birds occupied a restricted range under present conditions across the entire study area. All environmental variables considered were reduced to four uncorrelated factors for each species that explained a similar percentage of the total information: 97% for AG (100% of the marginality and 91% of the specialisation), 96% for GR (100% of the marginality and 91% of the specialisation) and 94% for UG (100% of the marginality and 87% of the specialisation).

The relative contributions of variables to the marginality factor were similar for AG and UG, but indicated a different pattern for GR (Table 2). The largest marginality scores showed that AG and UG select landscapes rich in cropland patches that are interconnected, and few select grazing field and native habitats (Table 2). In contrast, GR select landscape dominated by grazing lands that are interconnected with grazing and native patches, and few select croplands (Table 2). In addition, AG and UG occurred in areas more distant to towns and closer to waterbodies (Table 2). In contrast, GR showed a positive association with areas distant from lakes and ponds (Table 2). The highest specialisation of all species was associated with the edge density of the main land-cover types (Table 2) showing that these species may be less tolerant of habitat fragmentation.

Habitat Suitability Maps

Jack-knife validations indicated that all HSMs were highly reliable (rs > 0.95 for all species). In addition, the Boyce index (B ± SD) showed that model discriminations were better than random (0.95 ± 0.14 for UG, 0.79 ± 0.08 for GR and 0.65 ± 0.08 for AG). The final habitat-suitability maps showed that the major proportion of the study area was categorised as unsuitable habitat for all three species (Figure 2). Suitable areas for GR were located in the west and south of the study region, near the hills of the Ventania System, and along the coastal dunes of Buenos Aires province, and comprised 13% of the study area (Figure 2a). The suitable

TABLE 2

Contribution of environmental variables to the marginality and specialisation factor for Greater Rhea, Upland Goose and Ashy-headed Goose in the southern Pampas, Argentina. In the marginality factor, negative or positive coefficients indicate that the species is found in areas with lower (–) or higher (+) values than the average for the study area. The specialisation factor was calculated by sum of absolute contribution in all factors of ENFA pondered by the Eigenvalues of each factor.
[Contribución de las variables ambientales al factor de marginalidad y especialización para el ñandú común, el cauquén común, y el cauquén cabecigrís en el sur de la región Pampeana, Argentina. En el factor de marginalidad, los coeficientes negativos o positivos indican que la especie se encuentra en áreas con valores menores (–) o mayores (+) que el valor promedio en el área de estudio. El factor de especialización se calculó mediante la suma de la contribución absoluta de todos los factores de ENFA ponderado por el valor promedio de cada factor.]

	Marginality			**Specialisation**		
	Greater Rhea	Ashy-headed Goose	Upland Goose	Greater Rhea	Ashy-headed Goose	Upland Goose
Altitude	0.07	–0.12	–0.12	1.51	0.75	1.15
Crop.area	–0.35	0.38	0.43	1.99	1.55	1.61
Grazing.area	0.48	–0.33	–0.34	2.77	1.82	2.20
Native.area	0.11	–0.17	–0.19	2.45	1.19	1.74
Crop.edge	–0.11	0.02	0.11	3.30	2.71	3.03
Grazing.edge	0.07	–0.30	–0.20	3.41	2.75	3.28
Native.edge	0.23	–0.21	–0.19	4.60	2.23	2.85
Wetland.edge	–0.11	–0.10	–0.14	1.18	1.03	1.01
Dist.lake	0.49	–0.26	–0.32	2.33	0.80	0.99
Crop.con	–0.09	0.25	0.32	2.05	0.49	0.87
Grazing.con	0.33	–0.30	–0.26	0.78	1.75	1.89
Native.con	0.23	–0.28	–0.27	2.58	1.21	1.56
Slope	0.09	0.03	0.01	0.84	0.55	0.96
Dist.stream	0.02	–0.10	–0.18	1.21	0.43	0.54
Dist.urban	–0.37	0.50	0.40	1.15	0.75	1.06

areas for UG were especially concentrated in the central and eastern part of the study area, comprising 26% of this region (Figure 2b), while AG showed restricted suitable areas (6%) in the eastern part of the study area (Figure 2c).

Niche Overlap

The cross-tabulated habitat suitability map did not reveal areas classified as suitable habitat for the three species together (Figure 3). The shape of the ecological niches showed

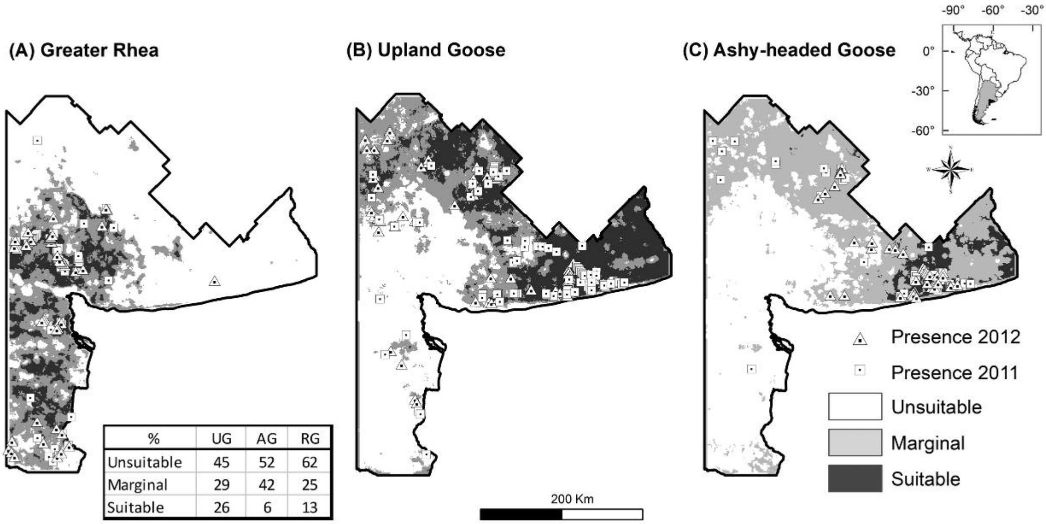

FIG. 2.—Habitat suitability maps for a) Greater Rhea (GR), b) Upland Goose (UG), c) Ashy-headed Goose (AG), in the southern Pampas, Argentina. Different colours identify three categories of habitat quality: unsuitable (white), marginal (grey) and suitable (black) developed for each species by applying ENFA. See supplementary material appendix 1, Figure A2 for a colour version.
[Mapas de adecuación del hábitat del a) ñandú común (GR), b) el cauquén común (UG) y c) el cauquén cabecigrís (AG) en el sur de la región Pampeana, Argentina. Diferentes colores identifican tres categorías de calidad del hábitat: inadecuado (blanco), marginal (gris) y adecuado (negro) desarrollado para cada especie aplicando ENFA. Veáse el material suplementario, apéndice 1, Figura A2 para una versión en color.]

that UG and AG niches overlapped widely over the eastern part of the study area and that suitable areas for UG were broader when compared to AG (Figure 2, 3). In contrast, regions classified as suitable for GR were restricted to the west and south of Buenos Aires province and along the coastline (Figure 3). It is important to note that areas classified as marginal for all species were located in the centre of the study area, embedded between suitable areas for GR and sheldgeese (Figure 3).

Results of the discriminant analysis of the ecological niches of species-pairs showed that GR presence is positively associated with large areas of grazing lands and native vegetation divided into small patches of grazing lands, in contrast to sheldgeese (Figure 4a, 4b). UG presence was associated with areas composed by small native patches embedded in areas with a large percentage of croplands, in contrast to GR (Figure 4a) and AG (Figure 4c). On the other hand, AG occurrence was correlated with large areas of croplands fragmented into small patches, in contrast to GR (Figure 4b) and to areas of croplands and grazing lands, in contrast to UG (Figure 4c).

DISCUSSION

Greater Rheas, Upland Geese and Ashy-headed Geese responded to landscape composition and configuration, as indicated by the high global marginality and the low proportion of the study area with suitable conditions for these medium-large birds found in this study. Greater Rhea and sheldgeese presented low niche overlap (only in marginal areas) in the southern Pampas during the non-breeding season (Figure 3). The low proportion of the landscape with suitable conditions for these native birds agrees with global trends that also suggest an increase in local extinction rates of their populations

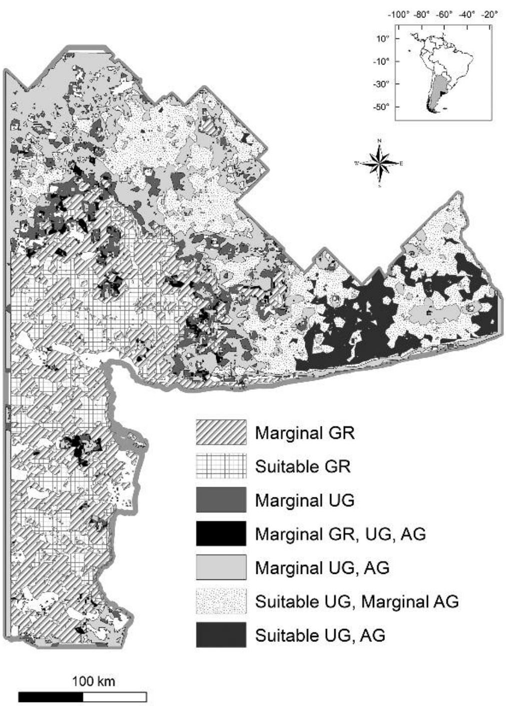

FIG. 3.—Niche overlap map between study species through crosstab analysis. Different letters identify the three species: Greater Rhea (GR), Upland Goose (UG), and Ashy-headed Goose (AG). See supplementary material appendix 1, Figure A3 for a colour version.

[Mapa de superposición de nichos entre las especies en estudio, mediante el análisis de tablas cruzadas. Diferentes letras identifican las tres especies: ñandú común (GR), cauquén común (UG) y cauquén cabecigrís (AG). Veáse el material suplementario, apéndice 1, Figura A3 para una versión en color.]

(Blanco & de la Balze, 2006; Bellis *et al*., 2004a; Giordano *et al*., 2010) and, in the case of the Greater Rhea, a decrease also in within-population levels of genetic variation (Bouzat, 2001). In comparison with the historical distribution data (Figure 1a, IUCN, 2017), we found that suitable and marginal areas for the Greater Rhea represented 65% of this area of the southern Pampas; for Upland Goose and Ashy-headed Goose they represented around 70%.

From the HSM of the three species in the study area we can suggest that: 1) land-use is the main driver for all species distribution: cultivated fields in the case of Ashy-headed and Upland Geese and grazing rangelands in the case of Greater Rhea; 2) connectivity between land-use patches is also an important landscape feature for species distribution; that is to say, high connectivity between cropland and grazing land patches for Ashy-headed and Upland Geese and for Greater Rhea, respectively; 3) urban areas may have a negative effect on sheldgeese distribution but have no clear effect on Greater Rhea distribution; and 4) waterbodies, such as small lakes and ponds, are preferred habitats for sheldgeese but Greater Rhea avoid this habitat.

In addition, the results achieved in this study have improved our knowledge and understanding of habitat requirements and ecological constraints across the distributional range of the three species since their differential responses to landscape transformation and fragmentation in the Pampas are probably associated with different life history traits. In the context of agricultural expansion over lands traditionally devoted to cattle ranching, supported by technological improvements (transgenic seeds, and high agrochemical input) and market factors (Baldi & Paruelo, 2008), Greater Rhea occurrence was linked mainly with areas composed by interconnected patches of grazing lands. Bellis *et al*., (2004b) and

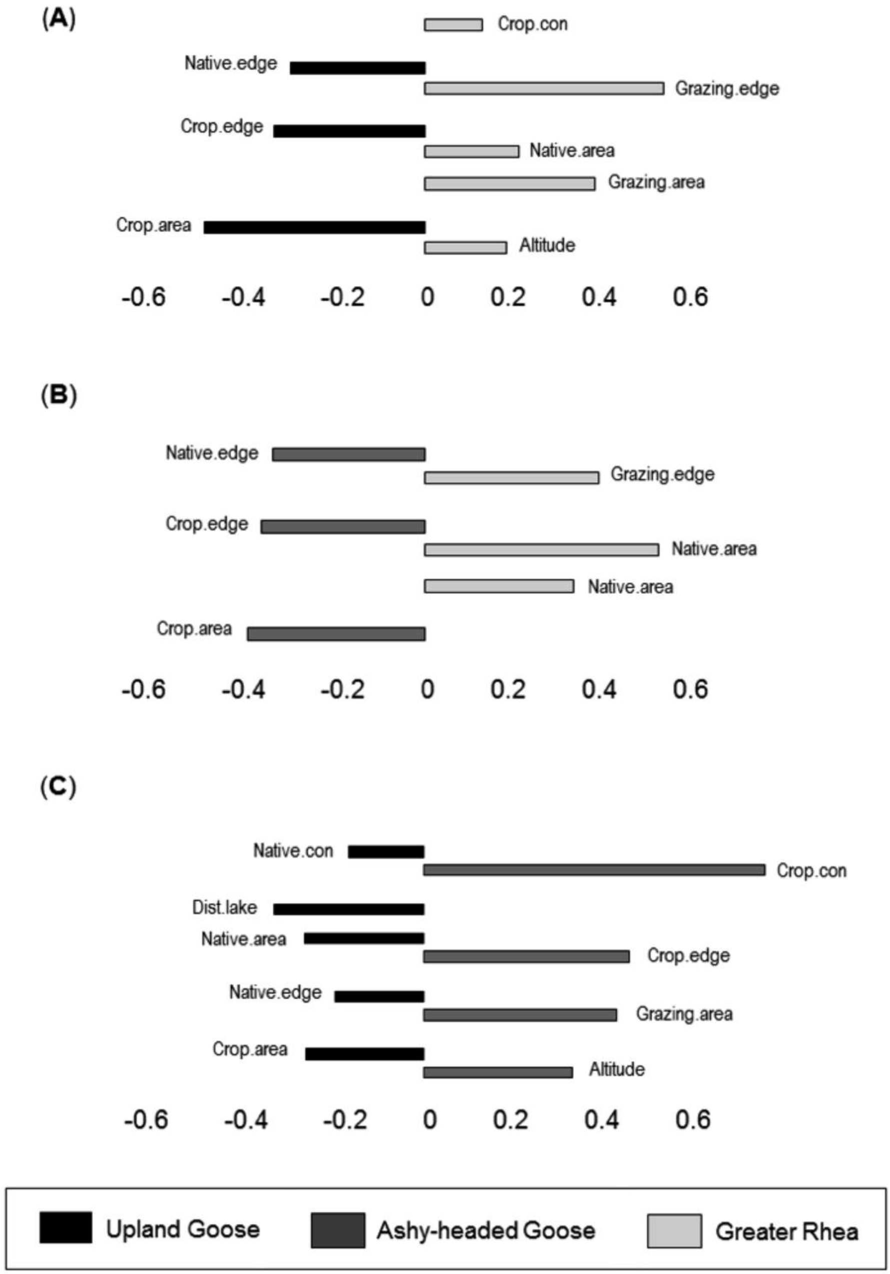

FIG. 4.—Coefficients of the discriminant function differentiating the ecological niches of species-pairs based on environmental variables: a) Upland Goose vs. Greater Rhea, b) Ashy-headed Goose vs. Greater Rhea, and c) Upland Goose vs. Ashy-headed Goose.

[Coeficientes del análisis discriminante que diferencian el nicho ecológico entre pares de especies en función de las variables ambientales: a) cauquén común vs. *ñandú común, b) cauquén cabecigrís* vs. *ñandú común y c) cauquén común* vs. *cauquén cabecigrís.]*

Giordano *et al*., (2010) postulated that Greater Rheas can adjust their movements and home range sizes in response to food availability. Meanwhile, the progressive loss of grasslands would affect the survival of the species, since it involves the loss or fragmentation of the optimal habitat for reproduction (Bellis *et al*., 2004a). In the case of the Greater Rhea, the main focus should be on preventing native habitat and current grazing rangelands replacement, which would surely also improve the conservation of a large group of native organisms. In the cases of the Upland Goose and Ashy-headed Goose, conservation strongly depends on stimulating human coexistence with these birds in agroecosystems, since these species select mainly cultivated areas that probably offer better forage than native habitats (Ackerman *et al*., 2006; Viglizzo *et al*., 2011). In summary, we found that species distribution was linked with contrasting environmental variables and it is therefore most important for the conservation of biodiversity to retain environmental heterogeneity, especially in view of the continuing expansion of soybean cultivation, which is leading to greater homogeneity in the agroecosystem matrix (Baldi & Paruelo, 2008; Viglizzo *et al*., 2011).

Current conservation efforts in the Pampas region mainly comprise the elaboration of management plans, the establishment of new reserves and the development of sustainable agricultural activities (Azpiroz *et al*., 2012). For instance, some areas classified as suitable for the Greater Rhea are included in the Ernesto Tornquist Provincial Park, a nature reserve in the west of the study area surrounded by the Ventania hills. In contrast, overlapping suitable areas for the Upland Goose and Ashy-headed Goose are not included in any protected area. Therefore, conservation of these species depends exclusively on adequate agroecosystem management and the effective prevention of illegal hunting. It is important to mention that the Ruddy-headed Goose *Chloephaga rubidiceps*, the smallest of the three species of migratory sheldgeese, is categorised as Critically Endangered in Argentina (López-Lanús *et al*., 2008) and has been declared a Provincial Natural Monument. As a result, further protection was also given to the other two migratory sheldgeese, since all three species winter together in the same area. Our results also help to identify the most suitable areas for the Ashy-headed Goose and Upland Goose, which in fact include the restricted distribution areas of the Ruddy-headed Goose. This information may be essential for decision-makers to identify priority areas for monitoring species' trends and controlling hunting activities.

Finally, there is current interest in promoting wildlife-friendly practices in agricultural lands by governmental and non-governmental institutions throughout the region. An example of this is the Alliance for the Grasslands (www.pastizalesdelconosur.org) initiative, which promotes certified beef production in natural grasslands. This initiative may offer a suitable opportunity to preserve grassland habitat for the Greater Rhea and to improve management practices of agroecosystems for sheldgeese. The development of sustainable agricultural activities promotes coexistence with humans and wildlife. Thus, this perspective may generate the resolution, or at least the minimisation, of conflicts with landowners who perceive a possible fall in income because of the presence of these species on their lands. Therefore, conservation programmes should use the HSM generated by this study to promote further studies of the development of mitigation measures associated with wildlife damage on crops, on working towards improving attitudes towards wildlife in agroecosystems and on improving management practices and carefully designed compensation schemes, which are tailored to local conditions.

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Supplementary Electronic Material

Colour versions of figures 1 to 3 may be found in the on-line version of this paper. See volume 65 (1) on www.ardeola.org

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